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Research Article

One is a worldwide invader, the other never established in other continents: contrasted phylogeographic patterns of two congeneric *Hylurgus* conifer bark beetles

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Abstract

In the Western Palaearctic, the congeneric bark beetles *Hylurgus ligniperda* and *Hylurgus micklitzi* are developing on pine trees. Although *H. ligniperda* has a larger native range in Europe, both species often occur in sympatry in the Mediterranean Basin. They share rather similar life histories, thus providing an excellent model for comparative studies on species differentiation and ecological traits. Moreover, along with increasing human activities and international trade, *H. ligniperda* has invaded all continents, whereas *H. micklitzi* remains confined to the Mediterranean Basin. Our research utilised COI markers to assess the genetic diversity and structure, alongside the demographic history, of both species and revealed marked differences. *H. micklitzi* exhibited low genetic diversity and shallow population structures with restricted expansion. In contrast, *H. ligniperda* displayed a longer and more complex post-glacial evolutionary route with four distinct clades originating from separate glacial refugia, coupled with considerable genetic variability across Europe. Comparative analyses about the two species suggest that species traits, such as larger body size, increased voltinism, broader ecological niches and frequent introduction events may have helped the fast global invasion and spread of *H. ligniperda* over the past century.

Key words: COI, comparative phylogeography, genetic structure, *Hylurgus ligniperda*, *Hylurgus micklitzi*, invasiveness, species traits

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Introduction

Globalisation has dismantled biogeographical barriers, accelerating the introduction of non-native insect species at an unprecedented rate over the past century without any sign of saturation for the future (Ricciardi 2007; Seebens et al. 2018). Plant trade has emerged as the predominant pathway for insect introductions (Liebhold et al. 2012; Fenn-Moltu et al. 2023), facilitating the establishment of numerous non-native species populations (Blackburn et al. 2011). When some of these species have become invasive, they pose significant threats to ecological

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systems and native biodiversity (CBD 2000). Additionally, they are responsible for substantial agricultural and forestry losses, incurring considerable economic costs related to their management and control (Ricciardi 2007; Bonnamour et al. 2021).

While some species successfully establish invasive populations across new regions, others, despite their phylogenetic and similar biological and ecological traits, remain confined to their native habitats. Comparing traits of related species with such differences would, thus, provide an opportunity to explore the mechanisms underlying the invasion processes. For instance, genomic comparisons of two congeneric species of *Spodoptera* (Lepidoptera, Noctuoidea) revealed potential factors contributing to the fall armyworm's successful invasion (Cui et al. 2020). Furthermore, Zhao et al. (2023) conducted a meta-analysis comparing traits of 100 invasive insects (including 25 Hemipterans, 23 Coleopterans, 18 Lepidopterans, 15 Hymenopterans and 12 Dipterans) with those of their non-invasive relatives, finding many differences in the number of introduction pathways, the number of habitats, life history traits, natural enemies and genomic traits. Compared to its congener *Dendroctonus ponderosae*, the invasive bark beetle *Dendroctonus valens* has a larger body size (Zhang et al. 2002; Pureswaran and Borden 2003; Shi and Sun 2010), more annual generations (Smith 1971; Bentz and Powell 2014), more and broader habitats (Smith 1971; Wood 1982; Salinas-Moreno et al. 2004), a larger genome size (Keeling et al. 2013; Liu et al. 2022) and a more complex phylogeographic pattern (Cai et al. 2008; Cullingham et al. 2012; Samarasekera et al. 2012; Taerum et al. 2016; Janes et al. 2018; Liu et al. 2022) in native areas.

Comparative phylogeography, which benefits from the improved integration of numerous complementary disciplines, including genetics, ecology, palaeontology, palynology and climatology, can identify geographical distributions and evolution of genetic lineages in sympatric species (Taberlet et al. 1998). On a large scale, the general trends across one certain region could be analysed and elucidated by comparing over the same area intraspecific phylogeographic patterns of several taxa (e.g. birds, reptiles, crustaceans etc.), including glacial refugia, post-glacial colonisation routes, presence of geographic barriers, main suture-zones and others (Avise et al. 1987; Bermingham et al. 1992; Taberlet et al. 1998). On a smaller scale, comparative phylogeography of species in sympatry could infer general or special patterns of evolutionary history associated with specific regions and their biotic or abiotic characteristics (Bermingham and Moritz 1998; Avise 2009; Mayer et al. 2015). Due to its rapid mutation rate and short coalescence time, mitochondrial DNA (mtDNA) has obvious advantages in determining a species' genetic diversity and phylogeographic structure. MtDNA sequences are the most popular genetic markers for phylogeographic research because they allow the application of phylogenetic tools and the genealogical approach to population-level enquiries (Brito and Edwards 2009). This approach has also been used to compare genetic diversity and population structure in invading populations versus native ones to identify potential source areas of invasion (Javal 2017; Bras et al. 2019; Lesieur et al. 2019; Urvois et al. 2023).

The red-haired bark beetle *Hylurgus ligniperda* J. C. Fabricius (Coleoptera, Curculionidae, Scolytinae) and its sister species *Hylurgus micklitzi* Wachtl constitute an interesting study case. Native to the Western Palaearctic, these phloeophagous pests are often found in sympatry on pine trees, mainly in the Mediterranean parts of their distributions. *H. ligniperda*, a temperate species, has expanded its range to nearly all continents (CABI 2021; Brockerhoff et al. 2025b), contrasting

sharply with *H. micklitzi*, which remains confined to the Mediterranean Basin without any records of introduction so far (El Khoury et al. 2019). Brockerhoff et al. (2014) used 13,828 border interception records from the U.S. and New Zealand (1949–2008) for 444 beetle species as proxies for arrival rates to model the arrival-establishment relationship, *H. ligniperda* and *H. micklitzi* at 244.5 and 0.4, respectively. All the scolytids interception data at U.S. ports of entry during 1985–2000 showed 217 interceptions for *H. ligniperda* and a single interception for *H. micklitzi* from five European countries (Haack 2002). Between 2003 and 2016, *H. ligniperda* was the second most frequently intercepted scolytids in ports of China, with 10,199 interceptions (Wang et al. 2018).

Different species' characteristics might explain their different invasiveness to some extent. In the native range, both *Hylurgus* species have been observed to be capable of development on five species of pine trees: *Pinus pinaster* Aiton, *P. pinea* L., *P. halepensis* Mill., *P. brutia* Ten. and *P. nigra* J.F. Arnold (Fabre and Carle 1975; Mendel et al. 1985; El Khoury et al. 2019; Gencal and Sarikaya 2023). Since two bark beetles are exclusively dependent on pines for feeding and reproduction, it could be hypothesised that their respective phylogeographic distribution, glacial refugial areas and further population expansions are consistent with their main host pines. Besides, the two *Hylurgus* species share similar feeding habits, ecological niches and reproduction systems, but differ in adult body length (*H. ligniperda*: 4–5.7 mm, *H. micklitzi*: 3.5–3.8 mm) (Grüne 1979), voltinism (*H. ligniperda*: 1–4 generations/year, *H. micklitzi*: 1 generation/year) (Fabre and Carle 1975; Mendel et al. 1985; Parra Emilfork 1996), native distribution (*H. ligniperda*: Europe, North Africa, West Asia, *H. micklitzi*: Mediterranean Basin) (El Khoury et al. 2019; CABI 2021), host range in native habitats (*H. ligniperda*: six main pine species, *H. micklitzi*: two main and three minor pine species) (Fabre and Carle 1975; Mendel et al. 1985; El Khoury et al. 2019; Gencal and Sarikaya 2023).

In this study, we hypothesise that differences in genetic diversity in the native range, combined with species-specific biological and ecological traits, have contributed to the distinct invasive capacities of these two congeneric species. Our study aimed to compare the genetic diversity and phylogeographic patterns of the two *Hylurgus* species in their native Western Palaearctic and to discuss whether contrasting species' characteristics between *H. ligniperda* and *H. micklitzi* would have influenced their respective success or failure in invasion.

Materials and methods

Insect sampling

From 2013 to 2024, adults of *H. ligniperda* and *H. micklitzi* were sampled from traps deployed in ports-of-entry and pine forests baited with either bark beetle pheromones or cerambycid pheromone blends supplemented with ethanol and α-pinene as described in Roques et al. (2023). Specimens of *H. ligniperda* were obtained from 120 sites located in 10 native European regions (mainland France, Corsica, mainland Italy, Sardinia, Hungary, Czechia, Spain, Portugal, Switzerland and Greece) and nine invaded countries distributed over five continents (Chile, Argentina, China, USA, New Zealand, South Korea, South Africa, Uruguay and Australia). *H. micklitzi* was obtained from 53 sites in seven native regions distributed around the Mediterranean Basin (mainland France, Corsica, mainland Italy, Sardinia, Spain

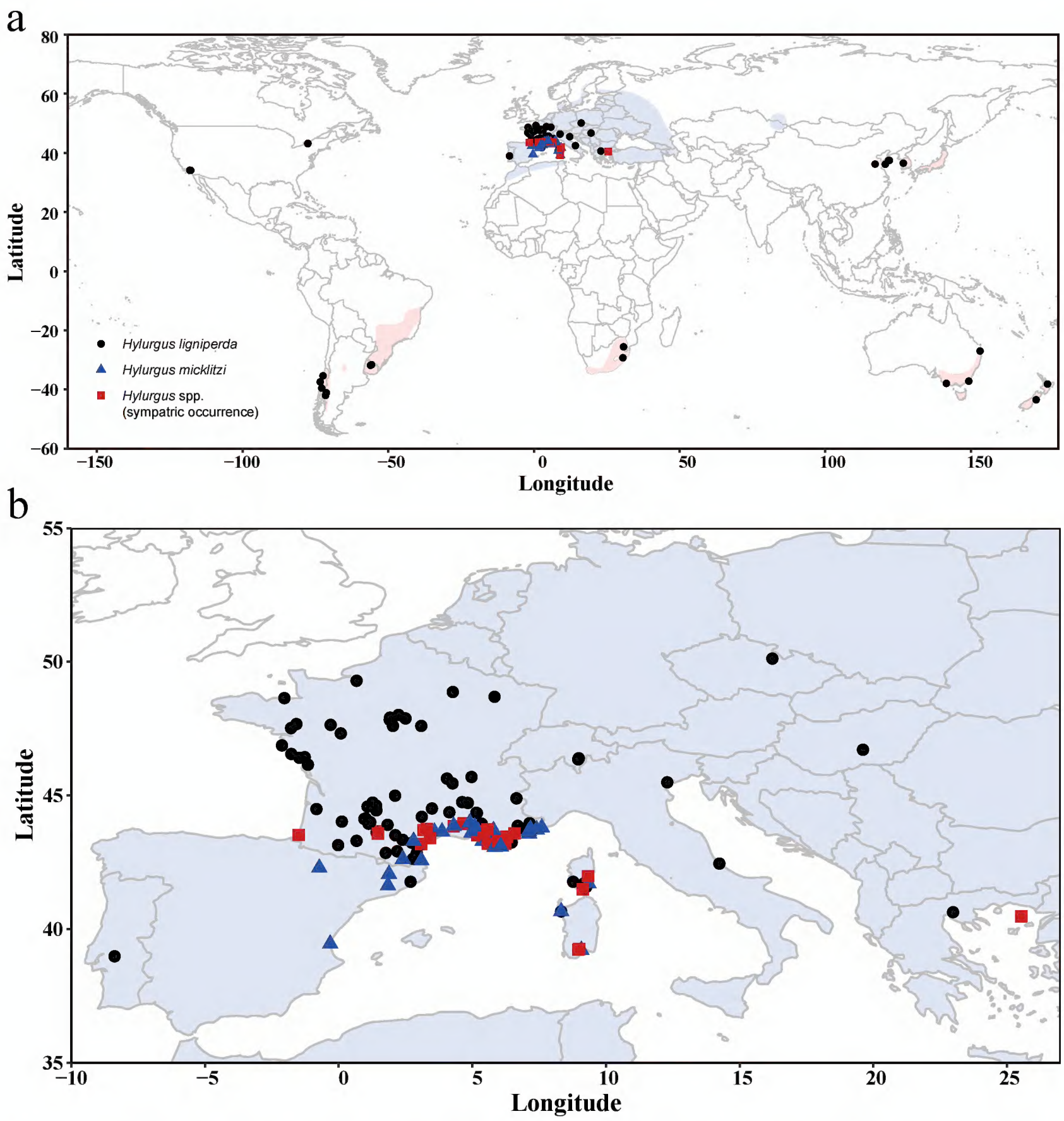

Figure 1. a. The sampling sites of *H. ligniperda* and *H. micklitzi* in the world; **b.** The sampling sites of *H. ligniperda* and *H. micklitzi* in Europe. Blue areas represent native ranges and red areas represent invasive ranges according to CABI and previous records for *H. ligniperda* (Parra Emilfork 1996; Kvamme and Lindelöw 2014; El Khoury et al. 2019; Lin et al. 2021; Lantschner et al. 2024; Brockerhoff et al. 2025b).

and Greece). The sampling locations are detailed in Fig. 1 and Suppl. material 1. Individuals were morphologically identified using the key available in Grüne (1979). All samples were stored in 96% ethanol and at -20 °C until DNA extraction.

DNA protocols, amplification and sequencing

For both species, DNA was extracted for 1–10 individuals from each sampling site using the DNeasy Tissue Kit (Qiagen, Hilden, Germany). The PCR reaction was amplified via the universal COI primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') for all individuals of two species (Folmer et al. 1994). The PCR was performed as follows: denaturation for 5 min at 94 °C followed by 35 cycles of amplification of 45 s at 94 °C, 50 s at 47 °C, 90 sec at 72 °C and final elongation for 5 min at 72 °C.

In order to check if the individuals were properly assigned to each species, we also amplified and sequenced a section of the conserved D1D3 domain of 28S rDNA from a representative number of specimens (*H. ligniperda*: N = 4; *H. micklitzi*: N = 1), using conserved forward primer D1F (5'-ACCCGCTGAATTTAAGCATAT-3') and reverse primer D3R (5'-TAGTTCACCATCTTTCGGGTC-3') (Harry et al. 1996, Lopez-Vaamonde et al. 2001). The PCR amplification consisted of the denaturation for 5 sec at 95 °C, followed by 35 cycles of 30 sec at 95 °C, 30 sec at 53 °C and 1 min 30 sec at 72 °C.

The purification of amplicons was performed with NucleoSpin gel and a NucloFast 96 PCR clean-up kit (Macherey-Nagel, Düren, Germany). All sequences were obtained in the forward and reverse directions on an ABI Prism 3500 Genetic Analyzer (Thermo Fisher Scientific) using the ABI Prism BigDye 3.1 Terminator sequencing Kit (Applied Biosystems, Foster City, CA, USA) and the primers used for PCR amplification. All sequence electropherograms were checked and we created contigs and trimmed all sequences to the same length using Codon Code Aligner 6.0.2 (CodonCode Corporation, Dedham, MA, USA). DNA sequences were aligned using ClustalW in MEGA11 (Tamura et al. 2021). The alignment was completed with seven COI sequences of *H. ligniperda* available from GenBank, from two sources, including sequences JQ015128–JQ015131 (Shukle et al. 2019) and MZ562956 and MZ562958 (Lin et al. 2021), one sequence of *H. micklitzi* is KM285773 (Rougerie et al. 2015).

Molecular data analyses

All sequences were translated into amino acids to check that no stop codons occurred; to quantify the divergence between haplotypes, the pairwise nucleotide *p*-distances were calculated by MEGA11 (Tamura et al. 2021). A Maximum-Likelihood phylogenetic tree using the Tamura 3-parameter (T92) + G Model was performed with 1,000 bootstraps by MEGA11 (Tamura et al. 2021). *H. micklitzi* was selected as the outgroup for the population genetic analyses of *H. ligniperda* due to its close phylogenetic relationship, while being a distinct, non-invasive congeneric species. Indices of genetic diversity in the studied species (gene diversity and nucleotide diversity per site) were estimated using DNAsp6 (Rozas et al. 2017). To identify groups of the population that were geographically homogeneous and maximally differentiated by a spatial analysis of variance, we used a spatial analysis of variance (SAMOVA 2.0) (Dupanloup et al. 2002). The programme was run for 10,000 permutations from 100 random initial conditions for 2 to 15 differentiated groups (K = 2 to K = 15). A TCS haplotype network, based on statistical parsimony, was built and lineage and haplotype maps were performed using R version 4.5.1 (R Core Team 2024). To infer the demographic histories and detect signs of recent population expansions, we used the frequency-based indicators Tajima's D and Fu's FS statistics available in DNAsp6 (Rozas et al. 2017). Significantly negative Tajima's D and Fu's FS values were taken as evidence of a population expansion.

Results

Interspecific study

The alignment of the 274 and 174 partial COI sequences of *H. ligniperda* and *H. micklitzi*, respectively, revealed 139 polymorphic sites (no deletions nor insertions),

of which 75 appear as diagnostic mutations separating the two species. The alignment of 898 bp sequences belonging to the 28S rDNA gene separated *H. ligniperda* and *H. micklitzi* by 32 polymorphic sites, all of which appeared as diagnostic mutations. In order to confirm the specific status of all specimens identified as *H. ligniperda*, four individuals of *H. ligniperda*, representative of the four main mtDNA haplogroups and one individual of *H. micklitzi*, were sequenced for the 28S rDNA gene. Sequences corresponding to two individuals from Gruissan (France) belonging to HLD07 mtDNA lineage, one from Yantai (China) belonging to HLA01 and one from Lupiac (France) belonging to HLA02 displayed the same 28S genotype, except for one ambiguous site showing a double peak (one from Gruissan belonging to HLD07, one from Yantai belonging to HLA01) at the diagnostic nucleotide. The interspecific genetic distances ranged from 15.9% to 17.5% for the COI gene and ranged from 3.6% to 3.7% for the nuclear gene. All identified haplotypes were deposited in GenBank (accession references PV701517–PV701783 of *H. ligniperda* and PV691892–PV692064 of *H. micklitzi* for the COI gene and PV888900–PV888903 of *H. ligniperda* and PV888956 of *H. micklitzi* for the 28S gene).

Hylurgus ligniperda genetic study

We obtained 46 mtDNA haplotypes from 120 populations and 274 individuals, with 66 variable sites out of the 578 bp sequenced. Overall haplotype and nucleotide diversities were 0.767 and 0.01276, respectively, 0.785 and 0.01226 in the native area and 0.681 and 0.0143 in the invaded area. We found two main haplotypes HLA01 (100 individuals from 45 populations) and HLD07 (86 individuals from 52 populations) and 25 local haplotypes (Suppl. material 1). In the native area, 41 haplotypes were found, including the two dominant haplotypes HLA01 (67 individuals from 33 populations) and HLD07 (69 individuals from 44 populations) and 21 local haplotypes (Suppl. material 1; Fig. 2). In the invaded area, 10 haplotypes were identified, including the two main and widely introduced haplotypes HLA01 (23 individuals from 11 populations) and HLD07 (17 individuals from 8 populations), four limited distributed haplotypes (HLC07, HLC10, HLD03, HLD08) and the other four unknown locations haplotypes (HLE01, HLE02, HLE03, HLE04) (Suppl. material 1; Figs 2, 3).

Overall, the Maximum Likelihood tree and the haplotype TCS network revealed five major groups of haplotypes: HLA, HLB, HLC, HLD and HLE (Figs 2a, 3). Clade HLA grouped haplotype HLA01 and several other less frequent haplotypes (HLA02-14), mostly from south-eastern France. Clade HLB and clade HLC included six (HLB01-HLB06) and 13 (HLC01-HLC13) less frequent haplotypes, respectively, widely distributed in Europe. Clade HLD gathered haplotype HLD07 and some other low-frequency haplotypes (HLD01-06, HLD08-09), mainly from south-western France. Clade HLE grouped four unique haplotypes (HLE01-04) corresponding to the GenBank sequences. The HLE haplotypes used in this study were derived from GenBank records, based on unidentified museum specimens and likely do not originate from USA populations.

The genetic distances ranged from 0.17% to 1.9% within clades and from 0.69% to 2.6% between clades, except for HLE, for which the inter-clade genetic distance reached 4.84% (Table 2).

We conducted demographic inferences within the whole dataset and clades, except HLE. For the whole data, Fu's Fs (-9.515, $P < 0.05$) was significantly negative

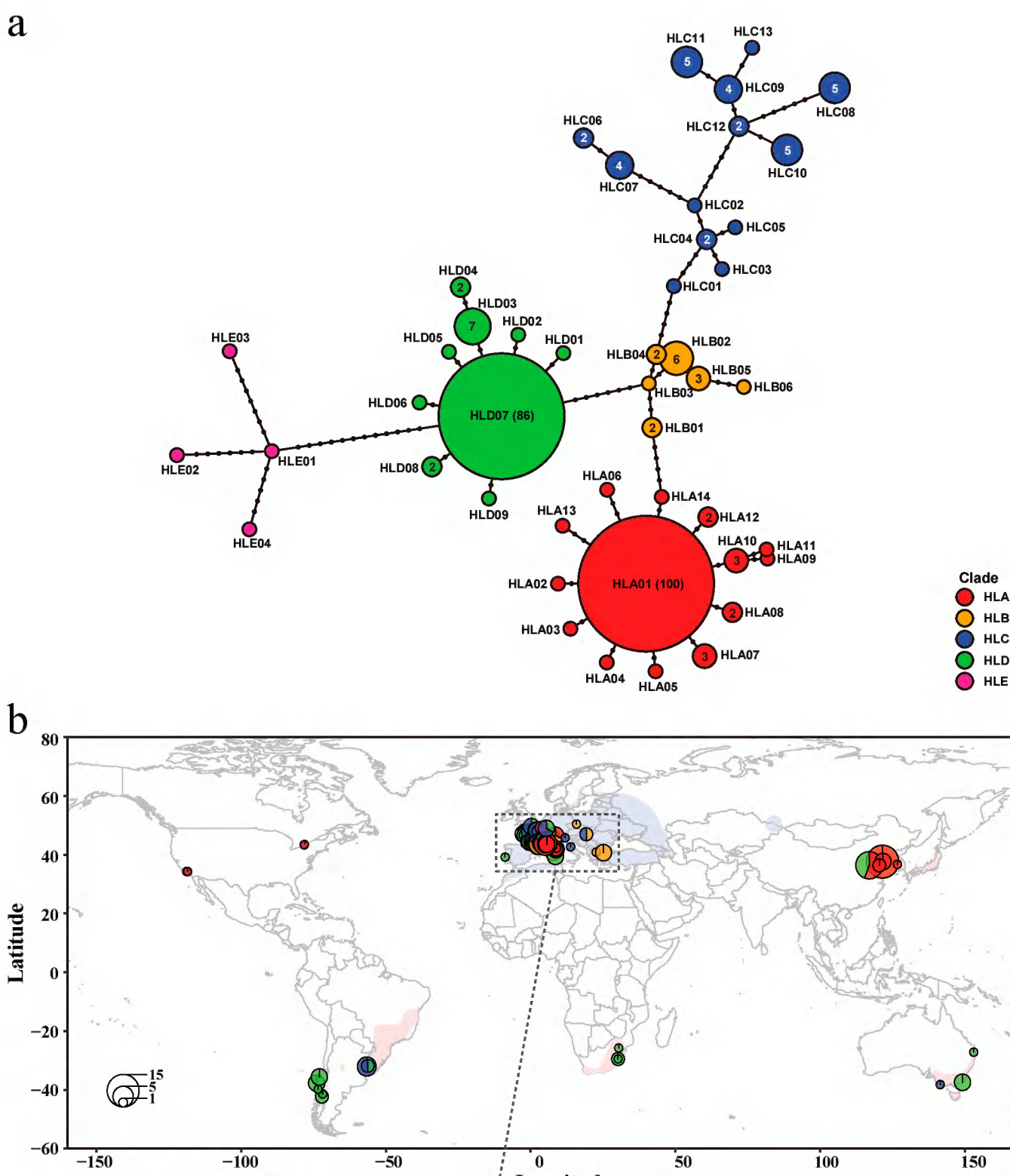

Figure 2. Geographical distribution of *H. ligniperda* populations and their associated COI haplotypes. **a.** TCS haplotype network found by the present study.The area of the circle represents haplotype frequencies (haplotypes without frequency annotations represent singleton sequences). Each black dot corresponds to a mutational step and each empty circle to a missing intermediate; **b.** The geographical distribution of the corresponding clades. The colours are the same as for the haplotype network above. Blue areas represent native ranges and red areas represent invasive ranges according to CABI and previous records (Parra Emilfork 1996; Kvamme and Lindelöw 2014; Lin et al. 2021; Brockerhoff et al. 2025b). HLE is not shown due to its unknown origin.

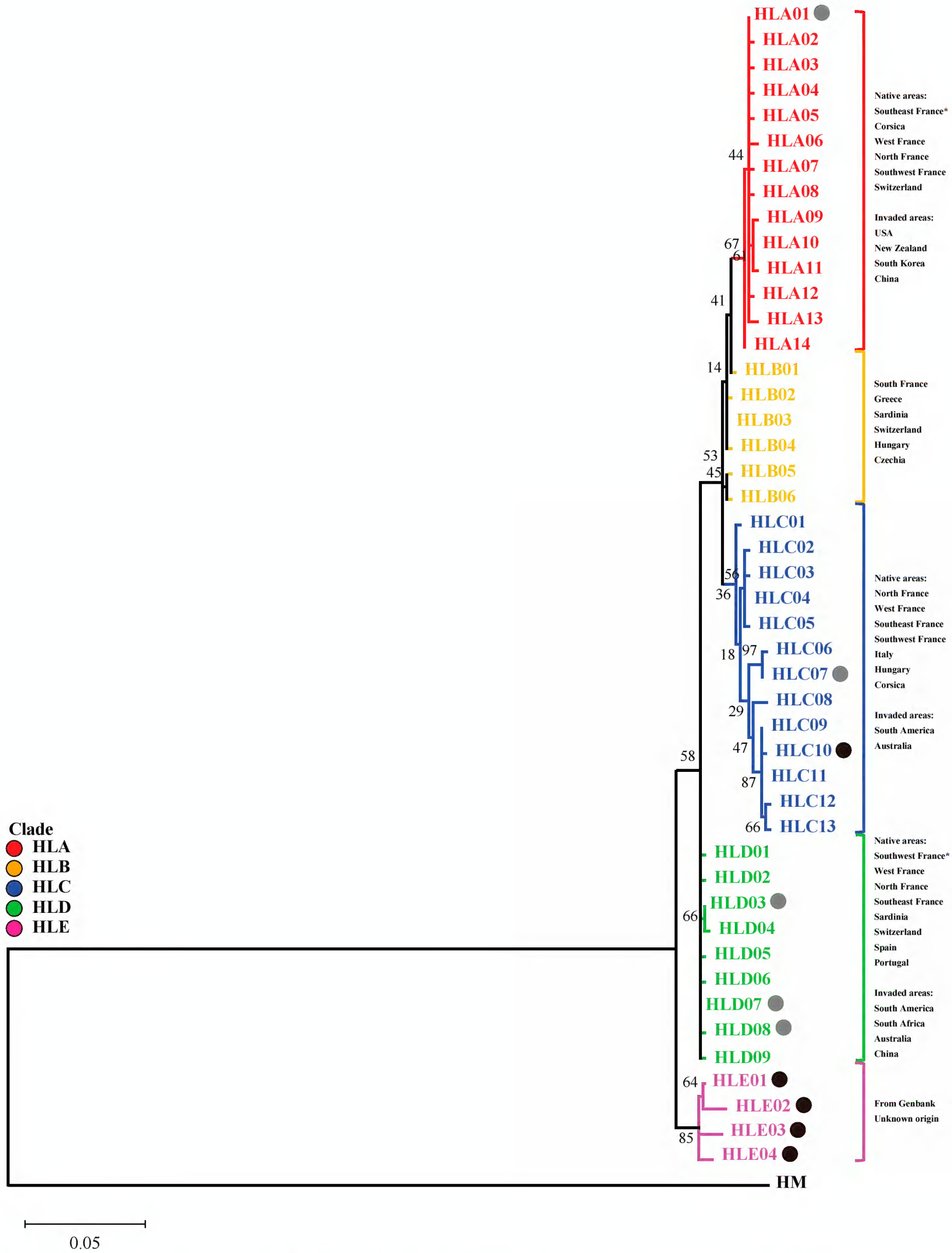

Figure 3. Maximum Likelihood tree (T92 + G Model), based on *H. ligniperda*'s COI sequences built with MEGA 11. *H. micklitzi* (HM) was used as an outgroup. The number beside the branch represents the the statistical support for that branch split. The colour of the squares next to the haplotypes shows whether they were identified in the native area only (no squares), in the invaded area only (black) or in both areas (grey). Asterisk indicates areas of widespread distribution for this lineage.

and for HLA and HLD, both Tajima's D values (HLA: -2.33698, $P < 0.01$; HLD: -1.88720, $P < 0.05$) and Fu's Fs (HLA: -18.446, $P < 0.01$; HLC: -9.058, $P < 0.05$) were significantly negative, indicating population expansion for these groups. By contrast, for HLB and HLC groups, results were not significant, indicating rather a long-term population demographic stability (Table 3).

Hierarchical analyses of molecular variance were performed using all individuals sampled from native areas (Europe). The five groups obtained with the SAMOVA analysis area shown in Fig. 4: (i) a 'south-eastern France' group comprising the 43 populations mainly in the east of Massif Central, Czechia, Switzerland and Corsica; (ii) a 'northern France' group clustering the six populations from northern France; (iii) a 'Greece' group including two populations from Thessaloniki, Greece; (iv) a 'central Europe' group comprising the four populations from north-western France, Hungary and mainland Italy; (v) a 'south-western France' group clustering the 39 populations from west of the Massif Central to the Pyrenees, the North Atlantic coast of western France, Spain, Portugal and Sardinia. The result showed that most of the molecular variance could be attributed to five geographical groups and within populations (67.19% and 32.38% respectively, $P < 0.001$).

Hylurgus micklitzi genetic study

MtDNA sequencing of 174 individuals from 53 populations resulted in an alignment of a 578 bp COI fragment, including 15 polymorphic sites and 16 haplotypes (Fig. 5a, Suppl. material 1). Haplotype and nucleotide diversities were 0.465 and 0.00096. One main haplotype, HM02 (N = 124), shared by three-quarters of the individuals, was distributed in most sampling locations in the western part of the Mediterranean Basin from Spain, southern mainland France and Corsica. A second, less frequent haplotype HM01 (N = 29) showed an extensive geographical distribution, occurring in the western (Spain, southern mainland France, Corsica and Sardinia) and eastern (Greece) part of the Mediterranean Basin.

The remaining 14 haplotypes (one to two individuals per haplotype) were observed in southern France (Fig. 5b). All other haplotypes were separated from the main haplotype HM02 by two mutation steps at most (Fig. 5a). The haplotype network was star-shaped and did not show any phylogenetic structure. We could identify one haplogroup of linked haplotypes (HM01-HM03-HM12-HM14-HM16) that mainly occurred in the western (Spain, southern mainland France, Corsica and Sardinia) and eastern (Greece) part of the Mediterranean Basin.

Given the absence of phylogenetic structure in *H. micklitzi*, the tests were only performed at the species level. Both Tajima's D (-2.03939, $P < 0.05$) and Fu's Fs (-17.176, $P < 0.05$) were negative and significant and unambiguously suggested a recent demographic expansion in this species.

Hylurgus species genetic study in sympatric sites

From 22 sites where the two species were trapped in sympatry (Fig. 1), we identified 14 COI haplotypes from 66 individuals of *H. ligniperda* and eight haplotypes from 50 individuals of *H. micklitzi* (Suppl. material 1). Overall, haplotype and nucleotide diversities were 0.675 and 0.00914 for *H. ligniperda* and 0.491 and 0.00112 for *H. micklitzi*. When comparing haplotype richness between the two

Table 1. The main species traits of *H. ligniperda* and *H. micklitzi*.

Species traits	*H. ligniperda*	References	*H. micklitzi*	References
Body size	4–5.7mm	(Grüne 1979)	3.5–3.8mm	(Grüne 1979)
Invaded distribution	China 2019, Argentina 2007, South Korea 1999, The United States 1995, Brazil 1991, Chile 1985, Sri Lanka (unknown date), New Zealand 1974, South Africa 1973, Uruguay 1956, Australia 1942, Japan 1935	(Murayama 1936; Bain 1977; Geertsema 1982; Ciesla and Ramírez Grez 1988; Wood and Bright 1992; Hoebeke 2001; Park et al. 2017; Kirkendall 2018; CABI 2021; Lin et al. 2021; Ren et al. 2021; Lantschner et al. 2024; Brockerhoff et al. 2025b)	/	/
Native distribution	Europe, northern Africa and West Asia	(Fabre and Carle 1975; CABI 2021; Brockerhoff et al. 2025b)	Around the Mediterranean Sea	(El Khoury et al. 2019)
Host plants	*P. pinaster*, *P. halepensis*, *P. sylvestris*, *P. pinea*, *P. brutia*, *P. nigra* in native areas; South Africa: *P patula*, *P elliottii*; Oceania: *P. radiata*; North America: *P. halepensis*, *P. pinea*; South America:*P. contorta*, *P. elliottii*, *P. ponderosa*, *P. radiata*, *P. sylvestris*, *P. taeda*; East Asia: *P. thunbergii*, *P. densiflora*	(Fabre and Carle 1975; Bain 1977; Zhou et al. 2001; Kim et al. 2011; Clare and George 2016; Lin et al. 2021; Ren et al. 2021; Gencal and Sarikaya 2023; Lantschner et al. 2024)	Mainly *P. halepensis* and *P. brutia*; Other: *P. pinaster*, *P. pinea*, *P. nigra*	(Mendel et al. 1985; Sarikaya and Yildirim 2011; Faccoli et al. 2020)
Initiate host location	Female	(Fabre and Carle 1975; Ren et al. 2021)	Female	(Mendel et al. 1985)
Feeding mode	Phloeophagous	(Vega and Hofstetter 2014)	Phloeophagous	(Vega and Hofstetter 2014)
Biological niches	Root and lower stem	(Fabre and Carle 1975)	Root and lower stem	(Mendel et al. 1985)
Sex ratio	F: M = 1: 1	(Lanfranco et al. 2001)	Unknown	/
Mating behaviour	Outbreeding and Inbreeding (to some extent)	(Fabre and Carle 1975)	Unknown	/
Parent adults in brood systems	Monogamous	(Ren et al. 2021)	Monogamous	(Mendel et al. 1985)
Voltinism	Uni- to multivoltine (1 ~ 4 generations/year)	(Fabre and Carle 1975; Tribe 1991; Parra Emilfork 1996; Ren et al. 2021)	Univoltine	(Mendel et al. 1985)
Fecundity	59 ~ 506 eggs per female in different host and temperature	(Fabre and Carle 1975; Ren et al. 2021)	Unknown	/
Dispersal capacity	Long distance (in the field): individuals were found ≥ 25 km from the nearest host patch; Short distance in the model prediction: 50% of the beetles were caught at 20 m, 305 m and 1150 m with GAMM and 123 m with GAM	(Chase et al. 2017; Meurisse and Pawson 2017; Brockerhoff et al. 2025a)	Unknown	/
Emergence temperature	9–20 °C (optimal 15 °C)	(Tribe 1991)	Unknown	/
Cold tolerance	The lowest SCP: -6.45 ± 0.18 °C (Shandong, China)	(Cheng et al. 2024)	Unknown	/
Development temperature	Eggs to larvae: 9–33 °C (optimal 27.5 °C); Larvae to pupae: 15–33 °C (optimal 28 °C); Pupae to adults: 15–33 °C (optimal 30 °C)	(Pugh et al. 2023)	Unknown	/
Aggregation pheromones	Unknown	/	Unknown	/
Primary (attack living trees)	Secondary	(Fabre and Carle 1975; Ren et al. 2021)	Secondary	(Mendel et al. 1985)
Tree killers	No	(Fabre and Carle 1975; Ren et al. 2021)	No	(Mendel et al. 1985)
Outbreaks	No	(Fabre and Carle 1975; Ren et al. 2021)	No	(Mendel et al. 1985)

Table 2. Minimum – maximum *p*-distances within and between species or clades of *H. ligniperda* and *H. micklitzi* (derived from the mitochondrial haplotypes).

Distance	HL	HLA	HLB	HLC	HLD	HLE	HM
HL	0.2%-4.9%						
HLA		0.2%-0.7%					
HLB		0.7%-1.7%	0.2%-0.9%				
HLC		1.0%-2.6%	0.7%-2.2%	0.2%-1.7%			
HLD		1.6%-2.6%	1.0%-1.7%	1.4%-2.4%	0.2%-0.5%		
HLE		3.8%-4.8%	3.1%-4.0%	3.5%-4.8%	2.1%-3.2%	0.9%-1.9%	
HM	15.9%-17.5%						0.2%-0.7%

Table 3. Tajima's D and Fu's FS values estimated for *H. ligniperda* (whole data set, HLA, HLB, HLC, HLD).

	n	Fu's FS	Tajima's D
whole dataset	274	-9.515*	-0.9425
HLA	119	-18.446**	-2.33698**
HLB	15	-0.274	0.50909
HLC	34	-1.166	0.30782
HLD	102	-9.058*	-1.88720*

n, number of individuals. Values in brackets correspond to the *P*-value. Asterisks indicate significant values (*: $P < 0.05$, **: $P < 0.01$).

species across the seven sympatric sites with equivalent sampling, *H. ligniperda* exhibited a greater number of haplotypes in three locations (La Londe-les-Maures, Toulouse and Bédarieux), whereas *H. micklitzi* showed higher richness only in Le Puy-Ste-Réparade.

Discussion

The observed patterns of population structure and genetic diversity of the two studied species gave additional support that species-specific traits may play a pivotal role in shaping genetic variation and distribution, both directly and indirectly, while also facilitating the survival, establishment and rapid dispersal of non-native insect species (Mayer et al. 2015; Zhao et al. 2023). We investigated the genetic structure and the demographic history of two congeneric species that could be found in sympatry at small geographic scales. Our results revealed: 1) contrasting phylogeographic patterns between *H. ligniperda* and *H. micklitzi* in their native Western Palaearctic ranges; 2) more genetic variability and structure in the invasive species *H. ligniperda* than in non-invasive species *H. micklitzi*; and 3) a probable relation between diverse species traits, such as body length, voltinism and ecological niche and the invasiveness of our focal species (*H. ligniperda*), that its species-specific characteristics having potentially facilitated its invasion in new regions.

Two congeneric species in sympatry in the Western Palaearctic

Both molecular markers, the 28S rDNA gene and COI mtDNA gene, allow an accurate delimitation of *H. ligniperda* and *H. micklitzi*. COI genetic distances be-

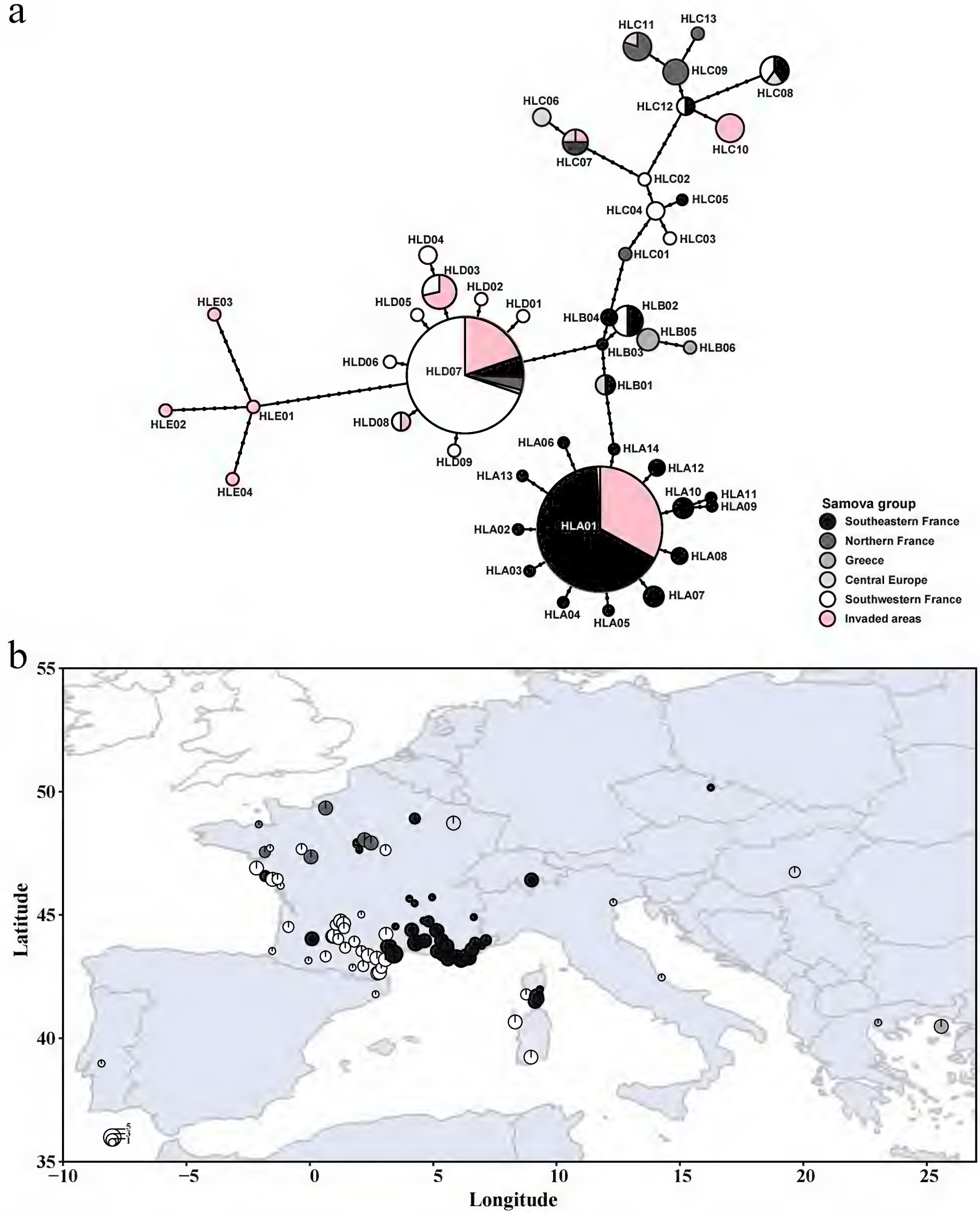

Figure 4. The Spatial Analysis of Molecular Variance (SAMOVA) results. **a.** Haplotype network of the 46 haplotypes of *H. ligniperda* shows the proportion of individuals belonging to each of the five groups and invaded areas; **b.** Geographical distribution of the five identified groups (see text for details) in native areas. The colours are the same as for the haplotype network above.

tween the two species ranged from 15.9% to 17.5%, which were higher than observed between other congeneric species of scolytids, based on the *p*-distance model. Within *Ips* bark beetles, Chang et al. (2012) found an interspecific genetic distance

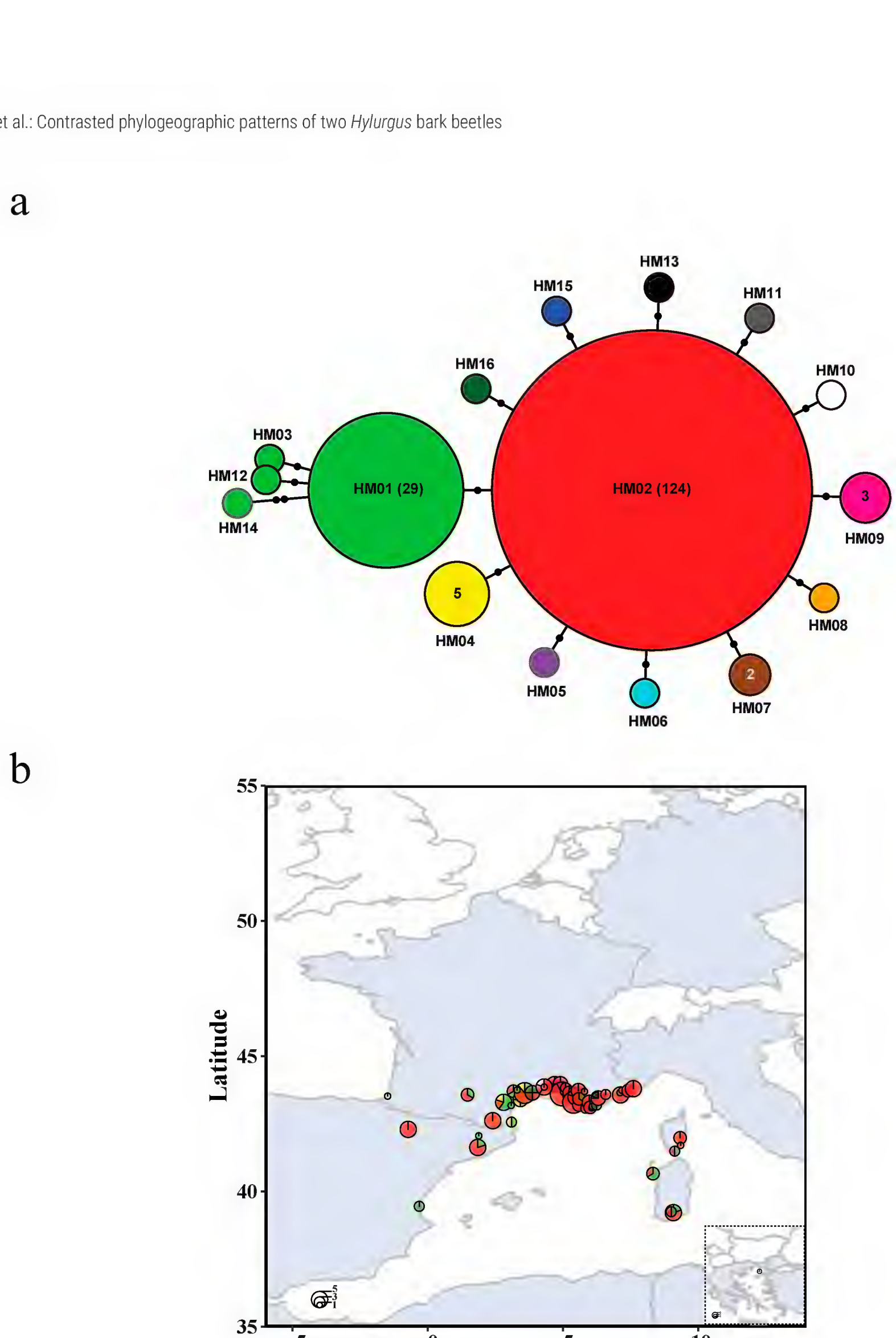

Figure 5. Geographical distribution of *H. micklitzi* populations and their associated COI haplotypes. **a.** TCS haplotype network found by the present study. The area of the circle represents haplotype frequencies (haplotypes without frequency annotations represent singleton sequences). Each black dot corresponds to a mutational step and each empty circle to a missing intermediate; **b.** The geographical distribution of the corresponding clades. The colours are the same as for the haplotype network above. Blue areas represent native ranges according to CABI and previous records (El Khoury et al. 2019; Lantschner et al. 2024).

between 5.6% and 43.1%, based on the Kimura 2-parameter (K2P) model for the COI gene. Du et al. (2021) found mitochondrial genome distances were 22.0% (*Hylastes* species), 9.0% (*Trypodendron* species), 16.9% ~ 23.6% (*Xylosandrus* species), 9.0% ~ 26.3% (*Dryocoetes* species), 24.5% (*Orthotomicus* species) and 3.7% ~ 22.2% (*Ips* species), based on the K2P model. Likewise, COI and COII genetic dis-

tances separating the *Tomicus* bark beetle species ranged from 10.7% to 12.4% between *Tomicus piniperda*, *Tomicus destruens* and *Tomicus minor* and reached 22.9% between *Tomicus* spp. and *Dendroctonus* spp., based on the K2P model (Kerdelhué et al. 2002). Analysing 33 genera and 258 species of ambrosia beetles (Xyleborini tribe) of southeast Asia, Cognato et al. (2020) observed an average interspecific difference for congenerics ranging from 9.3–16.3% for COI, based on *p*-distance model. The two species of *Hylurgus* under study may have been separated a long time ago. Due to a faster evolutionary rate (Saccone et al. 1999), mtDNA showed greater intraspecific variability than the nuclear gene and revealed several clades within *H. ligniperda*. This was also observed in the cave beetle *Speonomus normandi hydrophilus* (Coleoptera, Leiodidae) (Kocot-Zalewska et al. 2021). Surprisingly, intraspecific distances within *H. ligniperda* reached 4.84% (when comparing clade HLE to other clades), but these results should be taken with caution because our study included some sequences obtained from GenBank which could result from species misidentifications.

Contrasting phylogeographic patterns between the two sympatric *Hylurgus* species in the native areas

Consistent with our hypothesis, patterns of genetic structure contrasted between the two species of bark beetles. *H. micklitzi* had much less genetic diversity than *H. ligniperda* locally (i.e. within sample sites), regionally (i.e. sympatric areas) and over the whole sampling range of the species (Suppl. materials 1, 2).

H. ligniperda, a diverse and strongly structured bark beetle in its native range

The genetic structure of continental European populations of *H. ligniperda* consisted of four groups, two mainly in southern France and two spread over the sampling sites in Europe. MtDNA haplotype richness was greater in populations sampled around the Mediterranean Basin than those sampled in the northern latitude, consistent with the "southern richness and northern purity" pattern, in which many European species survived in southern refugia and experienced successive bottlenecks during post-glacial northward expansion (Hewitt 1999). In the western side of the Mediterranean Basin, the geographical distribution of *H. ligniperda* partially matched that of its main hosts there, namely *Pinus halepensis* (Gómez et al. 2001; Vendramin et al. 2021; Kurt et al. 2023) and *Pinus pinaster* (Theraroz et al. 2024). The beetle's genetic diversity distribution may be influenced by historical and environmental constraints, rather than direct host association and local adaptation, similar to the Mediterranean scolytid *T. destruens* (Horn et al. 2006). The split into two groups ('South-eastern France' and 'South-western France') forming a contact zone in the middle of the Massif Central, where no obvious physical barrier to dispersal occurs, was consistent with the general patterns of genetic structure and diversity observed in European insect taxa such as *Monochamus galloprovincialis* (Haran et al. 2018) and *Thaumetopoea pityocampa* (Rousselet et al. 2010), which followed the classical routes of European post-glacial history (Taberlet et al. 1998; Schmitt 2007; Habel et al. 2010). This suture zone might result from two distinct refugia reaching secondary contact, i.e. when populations with different genomes spread from their refugia encounter (Hewitt 1999). Alternatively, this secondary contact zone could be of a relatively recent origin, as artificial plantations have established a connection

between the native natural forests of *P. pinaster* in the west and *P. sylvestris* L. in the Massif Central (Rousselet et al. 2010). Greece showed two endemic haplotypes that could originate from another classical refuge in the Balkan Peninsula in the eastern Mediterranean (Taberlet et al. 1998), but our limited sampling could not allow further conclusions. Interestingly, Corsica and Sardinia included the two main haplotypes plus four other haplotypes that were shared by the nearby coast of France and Italy, suggesting gene flow between the mainland and these islands.

Based on our sampling in native regions, we observed a strong diversity and genetic structure of invasive populations of *H. ligniperda* in non-native countries. Amongst the 41 haplotypes identified in the native range, at least one of the two most dominant haplotypes (HLA01 and HLD07) was also present in many invaded countries. In addition, four distant lineages were observed over the invaded regions, even within the same small geographic area. These results suggested that *H. ligniperda* most likely repeatedly invaded different locations from various sources before dispersing locally, as it has been shown in other invasive species, such as the woodwasp *Sirex noctilio* (Boissin et al. 2012), the longhorned beetle *Anoplophora glabripennis* (Javal 2017) and the ambrosia beetle *Xylosandrus crassiusculus* (Urvois et al. 2023) in new regions.

Except for HLC10, all haplotypes observed in the invaded area could be found in native regions. Haplotype HLA01 was observed in New York, California, New Zealand, China and South Africa. HLD07 was detected in South America and China. About four other haplotypes, HLC07 was observed in Australia, HLC10 in Uruguay and HLD03 in Uruguay and South Africa. Various haplotypes co-occurred in Australia, Uruguay, Chile and China, suggesting multiple invasions of this species have occurred, like in the box tree moth *Cydalima perspectalis* (Bras et al. 2019). However, even if we observed a population genetic structure of *H. ligniperda* in its native range, mtDNA does not allow determining accurately the native origin of the invaded haplotypes and secondary spreads, nor haplotypes involved in potential bridgehead scenario. Using methods to infer invasion pathways (Guillemaud et al. 2010), together with higher resolution molecular markers, such as RAD sequencing, would permit the accurate determination of the genetic structure of this species in its native range, that would help in the understanding of the dynamics of the introductions.

H. micklitzi, a specialist bark beetle with low genetic diversity and a weak genetic structure

H. micklitzi exhibited drastically different genetic features when compared to *H. ligniperda*: a shallow genetic distribution pattern, as could be seen in other insect species, such as the bark beetle *Ips sexdentatus* (Avtzis et al. 2019) and two geometrid moths *Ourapteryx szechuana* and *Thyrinteina arnobia* (Lepidoptera, Geometridae) (Cheng et al. 2021; Nanini et al. 2024). Only 15 haplotypes were identified over the Mediterranean Basin with low genetic diversity. *H. micklitzi* was characterised by a widespread major haplotype (HM02) all over the sampling sites and many haplotypes only occurred in a single location. The star-shaped network with one over-represented haplotype and an excess of rare ones, as well as the demographic indices, suggested a recent expansion history following a drastic bottleneck (Hickerson et al. 2010) and local occurrence of new, recent haplotypes that probably emerged through mutation during the rapid expansion process (Petit et al. 2005). Genetic diversity was mostly found in Montpellier in southern France, as it was ob-

served in the nearby City of Bessan for *H. ligniperda*. The genetic structure patterns of *H. micklitzi* closely matched its main host pine *P. halepensis* in the western Mediterranean (Kurt et al. 2023). The populations of *H. micklitzi* were mostly monomorphic located on the line from the Pyrenees to Provence and Cote d'Azur. For the eastern Mediterranean, only one haplotype (HM01) was detected in Greece, where *Pinus brutia* and *Pinus nigra* were present. It is worth noting that Corsica and Sardinia contained two main haplotypes (HM01, HM02), but lacked endemic haplotypes, suggesting this species possibly did not have a long history there. Even after experiencing severe population declines, this species' ability to utilise a variety of hosts under survival pressure helped to sustain local populations. Given the apparent lack of genetic diversity and structure in the sampled populations, one could hypothesise that *H. micklitzi* may have recolonised from a single glacial refuge in the post-glacial period and that populations had experienced severe bottlenecks during interglacial periods. To date, no published data are available. Distribution data majorly based on French populations, additional Mediterranean population sampling, such as Spain, Greece, Italy, Turkey, North African countries, are needed to better understand the phylogeographic patterns of this species.

Are there traits favouring invasion potential in *H. ligniperda* and not in *H. micklitzi*?

By comparing species characteristics reported in literature between the invasive *H. ligniperda* and the non-invasive *H. micklitzi*, our findings support the hypothesis that *H. ligniperda* has a larger body size, higher voltinism, larger ecological niches and displays more events of introduction.

The body length of *H. ligniperda* and *H. micklitzi* ranges from 4 to 5.7 mm and 3.5 to 3.8 mm, respectively (Grüne 1979). Adult females of *H. ligniperda* are always the first to locate and attack pine hosts (Ren et al. 2021). A large body size in females is frequently linked to a high potential fecundity because of a larger abdomen that could hold more eggs. Coupled with the capability of inbreeding to some extent, it may help such a non-native species to quickly establish populations in invaded sites (Preziosi et al. 1996). Moreover, large beetles are able to infest large mature trees, while small beetles infest predominantly younger plants. In *Phloeosinus* bark beetles, the small European species *P. aubei* (= *P. bicolor*) and *P. thujae* infest young plants, while the larger Japanese congener *P. rudis* can kill mature trees (Moraal 2010).

Voltinism also differs between the two species. *H. ligniperda* shows one generation per year under cold climates, but their number could be up to four under warmer climates, while *H. micklitzi* only presents one generation per year in all parts of its range. *H. ligniperda* overwinters as an adult in Shandong, China, with its supercooling point (SCP) reaching the lowest (-6.45 ± 0.18 °C) in the mid-to-pose overwintering period; it does not survive beyond one day at -15 °C (1-day LLT_{50} = -7.1 °C) and its cold tolerance and overwintering survival are directly influenced by glycogen, lipids, proteins and cryoprotectants (trehalose and sorbitol) (Cheng et al. 2024). To date, no published data are available regarding the overwintering behaviour or thermal tolerance parameters (e.g. critical thermal maxima and minima or SCP) of *H. micklitzi*. The number of generations per year in an insect's life cycle is positively associated with the rate of spread (Fahrner and Aukema 2018) and a high fecundity required for fast population growth allows the initially small populations to establish

and expand rapidly (Jelbert et al. 2019). The same pattern is observed in *Dendroctonus* bark beetles where the invasive *D. valens* can produce up to three generations per year (Yan et al. 2005), while its congener *D. ponderosae*, a dominant pest in western North America, but without any invasion record elsewhere, is mostly univoltine, with semi-voltinism at high elevations and rare bivoltinism (Bentz et al. 2019).

H. ligniperda is also observed in more extensive ecological niches and infests more pine hosts than *H. micklitzi*, the latter mainly present close to the coast around the Mediterranean. *H. ligniperda* has a broader host range, infesting over 18 *Pinus* species. This increases its chances of being transported via wood trade, leading to more frequent interceptions and multiple introductions compared to *H. micklitzi* (Table 1). While no evidence is currently available, *H. micklitzi* might potentially expand its host range if introduced into novel environments, although this remains speculative and would require experimental validation. Similarly, the invasive bark beetle, *D. valens*, infests all pine species in the native areas (extending from Nova Scotia, Canada, west to California, USA and south through Mexico to Guatemala and Honduras) (Bright 1976; Furniss and Carolin 1977; Wood 1982; Cibrián Tovar et al. 1995) and four pine species in the invaded areas (China) (Yan et al. 2005; Liu 2020; Liu et al. 2021) and the non-invasive bark beetle *D. ponderosae*, infesting all native pine trees, except *Pinus jeffreyi* in the native areas (extending from Baja California Norte, Mexico, to northern British Columbia and western Alberta, Canada) (Wood 1982). Another example is given by the invasive bark beetle *T. piniperda*, infesting eight pine species in the native areas (the Palaearctic area from western Europe (Portugal) to east Asia (Japan)) (Masuya et al. 1998, 1999; Ritzerow et al. 2004; Faccoli et al. 2005; Lieutier et al. 2015) and five pine species in the invaded area (North America) (Långström et al. 1994; Sadof et al. 1995; Haack and Poland 2001; Haack et al. 2001) and non-invasive bark beetle *T. destruens*, infesting seven pine species in the Mediterranean Basin known at present (Gallego et al. 2004; Sarikaya and Avci 2010).

Conclusion

Contrasting genetic diversity and phylogeographic structures of two *Hylurgus* species in sympatric sites across the Mediterranean Basin revealed their different expanding directions and recolonisation routes in contemporary and post-glacial times. *H. ligniperda* showed higher genetic diversity and structure than *H. micklitzi*, locally (i.e. within sample sites), regionally (i.e. sympatric areas) and over the whole sampling range of the species. *H. ligniperda* has invaded new regions all over the world, while its congener has remained confined in its natural range. Together with the species' traits, i.e. a larger body size, a higher voltinism and a larger ecological niche, these characteristics may have enhanced its invasiveness, leading to recurrent invasion and spread of *H. ligniperda* all over the world.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Data curation: EM. Funding acquisition: MAAR. Project administration: MAAR, GR. Resources: LR, AR, EGB. Software: EM. Supervision: GR. Writing – original draft: YY. Writing – review and editing: NA, EGB, LR, JS, YL, GR, AR, MAAR.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Summary of the localities sampled and specimens used in the COI sequencing analyses of *H. ligniperda* and *H. micklitzi*

Authors: Yuan Yuan, Alain Roques, Emmanuelle Magnoux, Lili Ren, Eckehard G. Brockerhoff, Juan Shi, Youqing Luo, Na An, Marie-Anne Auger-Rozenberg, Géraldine Roux

Data type: xlsx

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Supplementary material 2

Summary of the localities sampled and specimens used in the COI sequencing analyses of *H. ligniperda* and *H. micklitzi* in sympatry

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Data type: xlsx

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